THE SALINITY TOLERANCES OF SOME ESTUARINE PLANKTONIC CRUSTACEANS [1]

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In estuaries, copepods are important members of the zooplankton and benthos, yet there is little experimental information on the extent to which these crustaceans can withstand dilution. Data are available for a few free-living copepods (Marshall *et al.*, 1935; Zinn, 1942; Ranade, 1957; Eltringham and Barnett, 1958; Barnett, 1959; Hopper, 1960; Matutani, 1962; Battaglia and Bryan, 1964) and recent work on female *Acartia* adults shows that closely related planktonic species can vary considerably in their ability to survive in waters of low salinity (Lance, 1963). Thus, it has been established that *A. tonsa* has a greater tolerance to dilution than *A. bifilosa* which is in turn more tolerant than *A. discaudata.* These results are particularly relevant to the field work of Jeffries (1962) who deduces that both temperature and salinity can be important factors influencing the seasonal succession of *Acartia* species. It is possible that certain young or spawning stages are more sensitive and have narrower survival limits than non-spawning adults (Bullock, 1958). An attempt has therefore been made to compare the salinity tolerances of male and female adult copepods and of young stages in the life-history of copepod, decapod and cirripede species. Animals were taken from Southampton Water, which receives a flow of fresh water from three rivers, and investigated in the laboratory.

Materials and Methods

Tow-nettings were taken from Southampton Water during the high tides, transported to the laboratory, and stored in Plymouth sea water (salinity 36.0–36.9‰) at a temperature close to that recorded in the estuary at the time of collection. The following animals were sorted from the nettings: adults and occasionally copepodites of various copepod species, namely *Acartia bifilosa* (Giesbrecht), *A. clausi* Giesbrecht, *A. discaudata* (Giesbrecht), *A. tonsa* Dana, *Centropages hamatus* (Lilljeborg), and *Temora longicornis* (Muller); young developmental stages of the decapod crabs *Carcinus maenas* Pennant and *Porcellana longicornis* (Linnaeus) and of the cirripede *Elminius modestus* Darwin. Sorted animals were fed, maintained at field temperature, and finally used for experiments 24 hours after capture.

All adult copepods (including the potential carnivores) were fed with the green flagellate, *Dunaliella*, and no animal food was provided. Larvae of the copepods and of *Elminius* were given the diatom, *Phaeodactylum*, as food. All plant cells were cultured in Erdschreiber medium (Gross, 1937) and only cultures in the exponential

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phase of growth were used. *Porcellana* zoeae were provided with pieces of *Mytilus* mantle together with *Phaeodactylum*, whereas the post larvae were given *Mytilus* mantle only. Although plant cells and live animal food are suitable for *Carcinus* zoeae, only *Phaeodactylum* was available. *Mytilus* tissue was fed to the megalopa stages of *Carcinus*.

The salinity tolerance (*i.e.*, the ability to withstand dilution) of a species was determined according to the method described by Lance (1960, 1963). In each experiment, groups of animals were taken from full-strength sea water and placed directly into various dilutions. Each dilution, which can be expressed as a percentage of full-strength sea water, differed from its immediately higher or lower salinity in the range by 10%, 5%, or occasionally 2.5% sea water. Survival of the animals in diluted sea water was compared with that of individuals which were retained in full-strength sea water throughout. For each salinity, usually 50 animals were placed in 200 ml. of water. In the experiments using copepodites, however, sorting was very difficult and the numbers of larvae put in each vessel varied. Dead specimens were counted and removed at intervals, the first inspections being made after 20 hours. Preliminary tests had shown that there was little variation in survival between multiple runs and therefore only a single determination was made in each experiment. Plant food, when used, was maintained at a concentration of about 100,000 cells/ml. *Acartia* is most tolerant of dilution when the experimental and prevailing field temperatures are close, and least tolerant when the two temperatures differ markedly (Lance, 1963). Laboratory temperatures were therefore kept close to those recorded in the estuary at the time of collecting tow-nettings.

Results

The range of dilutions causing deaths was identified for each species by observing the general trends in survival for the entire experimental period. Experiments lasted for three to 14 days, and in the longest runs, the general results obtained after three days rarely differed, and then only slightly, from those recorded later. Hence, although the period of observation varied, the results of different experiments can be readily compared. In each experiment, survival in 100% sea water and in diluted sea water at the upper end of the salinity range was similar. At the lower salinities, however, deaths associated with dilution effects occurred. The number of deaths progressively increased according to the degree of dilution and no individuals survived at the lowest salinities. The survival of animals in undiluted sea water was generally good. The full details of results obtained for each species are reported elsewhere (Lance, 1960).

Those dilutions which caused the death of at least 50% of the animals during the initial 20 hours of exposure are arbitrarily termed "lethal" salinities. The following formula has been used for calculating survival values for this 20-hour period:

$$\% \text{ survival in diluted sea water} = \frac{a_1}{b_1} \times \frac{b_2}{a_2} \times 100$$

where a_1 = number of survivors in diluted sea water, a_2 = number of animals initially placed in diluted sea water, b_1 = number of survivors in full-strength sea water, b_2 = number of animals initially placed in full-strength sea water.

Adult copepods of both sexes

Results are given for adult males and females of *Acartia discaudata, A. clausi,* and *Centropages hamatus* in Table I. For each species, a wider range of salinities was lethal to the males, indicating that they were less tolerant of dilution than the females. Furthermore, the range of salinities causing mortality was greater for the males of both *Acartia* species, though *Centropages* showed no difference between sexes. The consistently higher survival of the females is emphasized in Figure 1, which compares the data obtained for copepods after they had been exposed to dilutions at the lower end of the salinity range for 20 hours.

TABLE I

Salinity tolerances of copepods

Species	Stage in life-history	Experimental temperature (° C.)	Range of salinities causing mortality (% sea water)	Range of lethal salinities (% sea water)
Acartia discaudata	adults			
	female	16.0	0–35	0–25
	male	16.0	0–40	0–30
Acartia clausi	adults			
	female	15.2	0–45	0–35
	male	15.2	0–55	0–45
Centropages hamatus	adults			
	female	13.5	0–55	0–35
	male	13.5	0–55	0–45
Acartia tonsa	adults			
	female	17.0	0–25	0–10
	copepodites Stage I, II, III, IV	17.0	0–25	0–20
Acartia bifilosa	adults			
	female	10.0	0–40	0–20
	copepodites Stage I + II	10.0	0–40	0–20

The results for *Centropages* are unusual in that this is the only copepod species which survived less well in full-strength sea water than in dilutions at the upper end of the salinity range. Thus, very few deaths (90–96% survival after $8\frac{1}{2}$ days) occurred in a salinity range of 90–60% sea water whereas only 60–62% of the copepods survived in undiluted sea water.

Copepodites and adult female copepods

The salinity tolerances of *Acartia tonsa* and *A. bifilosa* copepodites are compared with those of adult females in Table I. For *A. tonsa,* a smaller range of dilutions was lethal to adults than to Stage I, II, III, or IV copepodites, but otherwise each species yielded similar results for its adults and larvae. Differences become appar-

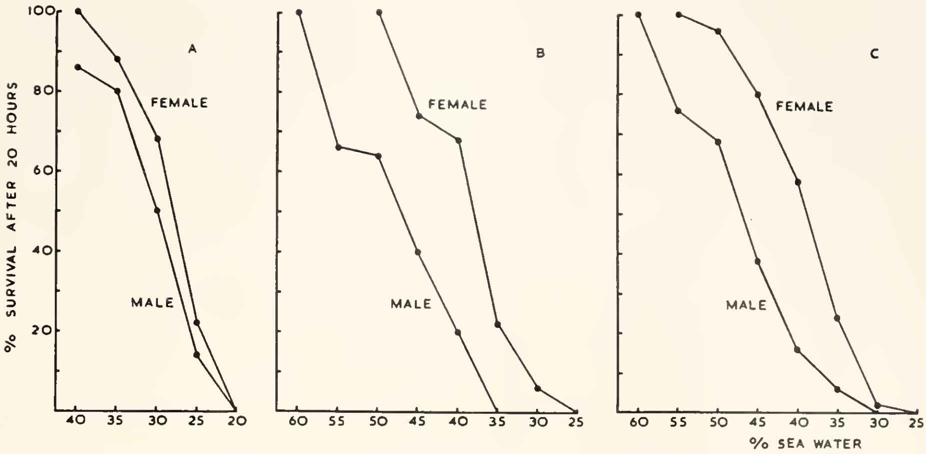

FIGURE 1. Per cent survival of adult copepods after 20 hours in diluted sea water. A, *Acartia discaudata*. B, *A. clausi*. C, *Centropages hamatus*.

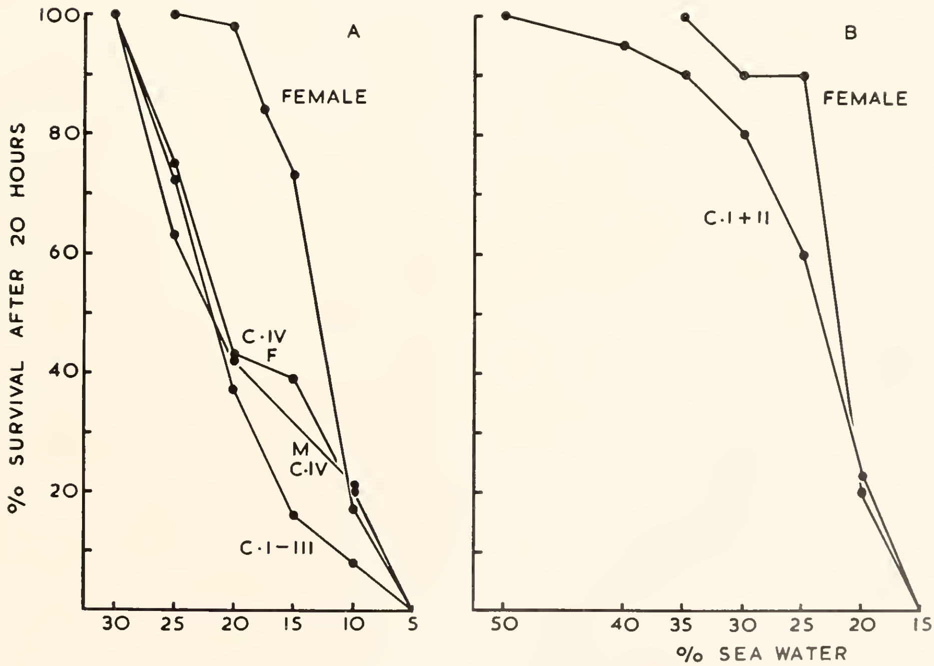

FIGURE 2. Per cent survival of copepodites and adult females after 20 hours in diluted sea water. A, *Acartia tonsa*. B, *A. bifilosa*. C, I–IV = copepodite stages; M = male; F = female. Insufficient *A. bifilosa* copepodites were available to justify analysis of the stages separately. *A. tonsa* Stage I, II, and III copepodites gave similar results and a mean survival value is plotted for each salinity.

Table II

Salinity tolerances of cirripedes and decapods

Species	Stage in life-history	Experimental temperature (° C.)	Range of salinities causing mortality (% sea water)	Range of lethal salinities (% sea water)
Elminius modestus	Stage VI nauplius	16.2	0–35	0–30
Carcinus maenas	Stage I zoea	17.0	0–90	0–35
	Megalopa	17.0	0–45	0–27.5
Porcellana longicornis	Stage I zoea	17.0	0–65	0–40
	Stage II zoea	17.0	0–65	0–40
	Post larva	17.0	0–70	0–57.5

ent, however, if survival after 20 hours is assessed (Fig. 2). With *A. tonsa* (Fig. 2 A), survival of adult females exceeded that of all larval stages in dilutions ranging from 15% to 25% sea water; in 10% sea water, survival was similar to that of Stage IV copepodites only, implying that these copepodites were less sensitive to dilution than the younger larvae. With *A. bifilosa* (Fig. 2 B), Stage I + II copepodites were slightly less tolerant than females in certain dilutions.

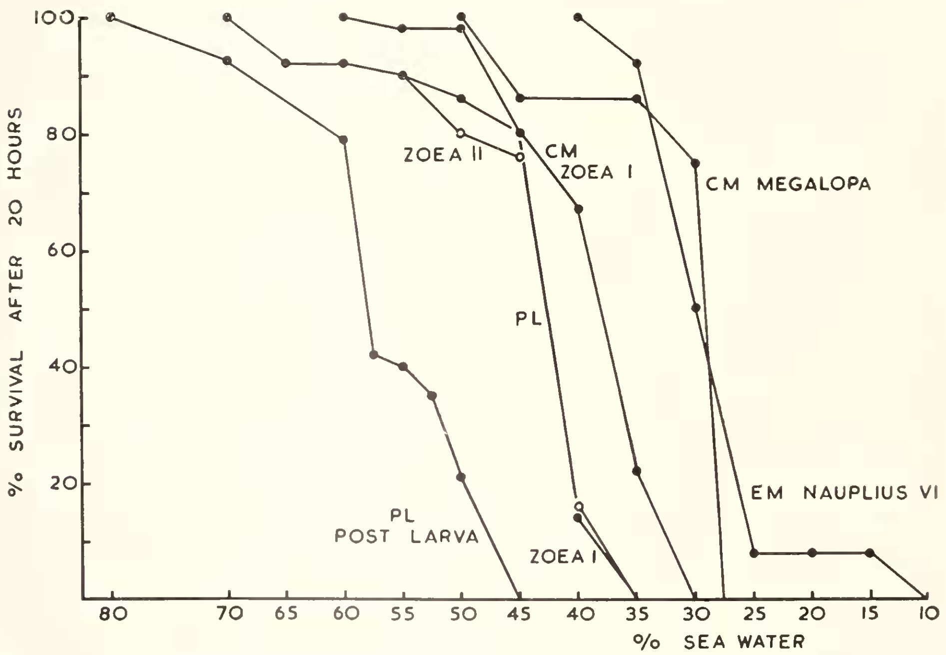

Figure 3. Per cent survival of decapod and cirripede developmental stages after 20 hours in diluted sea water. CM = *Carcinus maenas*; EM = *Elminius modestus*; PL = *Porcellana longicornis*.

Developmental stages of decapods

Table II presents data obtained from *Carcinus* Stage I zoeae and megalopa post larvae. The experiments using the megalopas are preliminary, as only a few animals were available. The zoeae were less resistant to dilution than the older megalopas. Figure 3, showing survival after 20 hours, demonstrates the greater susceptibility of the zoeae to water of lowered salinity. All megalopas surviving at salinities greater than 30% sea water moulted into crabs. Some megalopas moulted successfully in 30% sea water but others died while attempting to metamorphose; no moults occurred in the lethal salinities.

Results are included in Table II for *Porcellana*. It appears that Stage I and II zoeae had similar salinity tolerances and that they were more resistant to dilution than older post larval stages. This trend is obvious in Figure 3. In a further experiment lasting for two days, Stage II zoeae which were ready to moult into post larvae were used. Fewer moults occurred in 70% sea water than in media of higher salinity and none took place in 65% sea water or below.

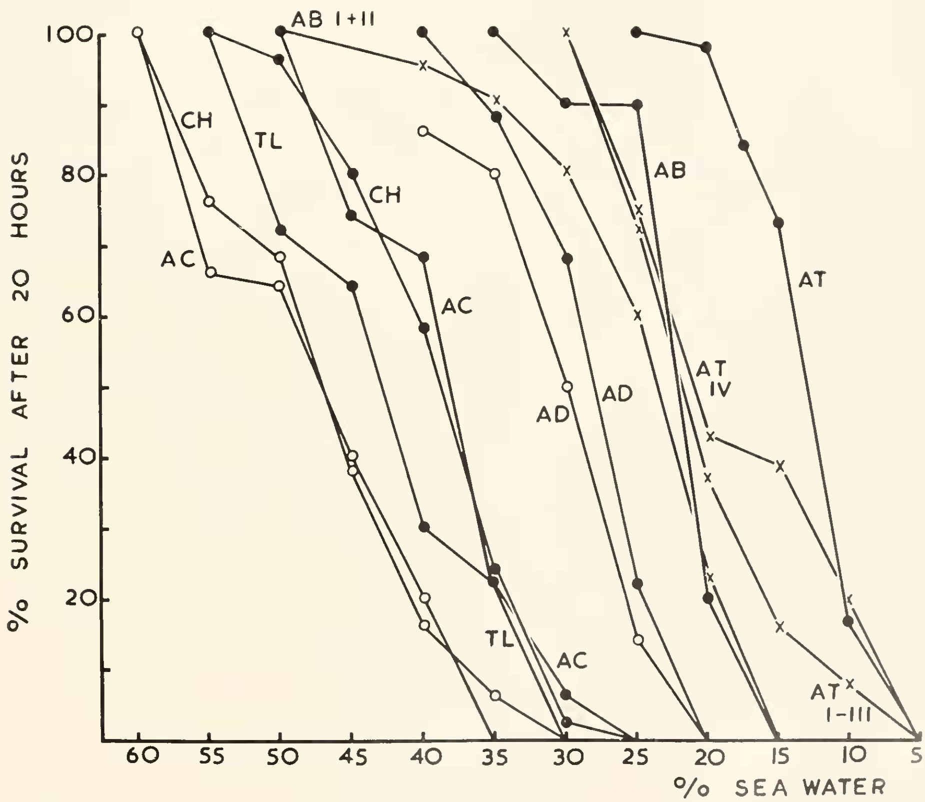

FIGURE 4. Per cent survival of copepods after 20 hours in diluted sea water. AB = *Acartia bifilosa;* AC = *A. clausi;* AD = *A. discaudata;* AT = *A. tonsa;* CH = *Centropages hamatus;* TL = *Temora longicornis;* black circle = adult females; white circle = adult males; cross = copepodites, Stage I, II, III, or female IV.

Larvae of cirripedes

Tests were confined to Stage VI nauplii of *Elminius*. Mortality occurred at salinities below 40% sea water and a range of 0–30% sea water was lethal (Table II, Fig. 3). During the experiment, many nauplii developed into cyprids. Thus, at salinities ranging from 100% to 50% sea water, the number of larvae moulting successfully into cyprids during the initial 20 hours varied between 24% and 46%. After 5 days at 100–55% sea water, 96–100% had moulted, as against 84% for 50% sea water. In 45% sea water, only 12% moulted during the first 20 hours but the number rose to 80% after 5 days. The nauplii in the remaining dilutions tended to swell and become immobile. Moulting was further delayed in both 40% and 35% sea water, and although all the nauplii in a range of 40–50% sea water had eventually become cyprids within 9 days, only 85% of the nauplii surviving in 35% sea water metamorphosed. No moults occurred at the lethal salinities. All the cyprids except for some of those in 40% and 35% sea water survived over a 7-day period following their initial appearance.

Comparison of salinity tolerances

Results obtained for all crustaceans, including those already discussed, can be compared in Figures 3 and 4 which show survival after exposure to diluted sea water for 20 hours. Relevant data are presented in Table III, where the different groups of animals have been arranged in a definite order according to their salinity tolerances. This order has been assessed by collating the 20-hour graphs and the data in Table III. Those animals with the greatest resistance to dilution are placed at the top of the list and those with the poorest salinity tolerances are assigned to the bottom.

TABLE III

Salinity tolerances of zooplankton taken from Southampton Water

Species	Stage in life-history	Field temperature at time of collection (°C.)	Experimental temperature (°C.)	Duration of expt. (days)	Range of salinities causing mortality		Range of lethal salinities	
					(% sea water)	(‰*)	(% sea water)	(‰*)
Acartia tonsa	adult female+	19.7	20.0	8	0–15	0– 5.4	0–10	0– 3.8
Acartia tonsa	adult female+	19.7	17.0	8	0–25	0– 9.1	0–10	0– 3.8
Acartia tonsa	Stage I–IV copepodite	19.7	17.0	5	0–25	0– 9.1	0–20	0– 7.4
Acartia bifilosa	adult female+	8.1	10.0	9	0–40	0–15.1	0–20	0– 7.8
Acartia bifilosa	Stage I+II copepodite	8.1	10.0	3	0–40	0–15.1	0–20	0– 7.8
Acartia discaudata	adult female+	15.3	16.0	5½	0–35	0–12.7	0–25	0– 9.3
Elminius modestus	Stage VI nauplius	17.2	16.2	5	0–35	0–12.3	0–30	0–10.3
Acartia discaudata	adult male	15.3	16.0	5½	0–40	0–14.8	0–30	0–11.2
Carcinus maenas	megalopa	17.0	17.0	14	0–45	0–15.9	0–27.5	0– 9.9
Acartia clausi	adult female	16.1	15.2	3	0–45	0–15.8	0–35	0–12.5
Centropages hamatus	adult female	15.0	13.5	8½	0–55	0–20.2	0–35	0–13.1
Carcinus maenas	Stage I zoea	17.0	17.0	7	0–90	0–33.0	0–35	0–12.5
Temora longicornis	adult female	15.3	14.1	5½	0–50	0–18.1	0–40	0–11.7
Porcellana longicornis	Stage I–II zoea	18.3	17.0	3½	0–65	0–23.9	0–40	0–11.8
Centropages hamatus	adult male	15.0	13.5	8½	0–55	0–20.2	0–45	0–16.3
Acartia clausi	adult male	16.1	15.2	3	0–55	0–19.2	0–45	0–15.8
Porcellana longicornis	post larva	**	17.0	6	0–70	0–25.6	0–57.5	0–21.0

+ Results published in 1963.
* Salinity value determined by titration.
** Reared from Stage II zoeae and used 12 hours after appearance.

Discussion

The experiments on *Acartia* and *Centropages* indicate that adult males are less tolerant of dilution than the females. A survey of zooplankton changes occurring in Long Island Sound has led Conover (1956) to suggest that unfavorable conditions probably affect the male *Acartia* first and his field evidence is therefore particularly relevant. As the survival of copepods in diluted sea water partly depends on the sex, it is not surprising that the influence of dilution on swimming behavior also differs between males and females (Lance, 1962). Thus, it is the males which show the most marked changes in vertical distribution when the salinity of sea water is lowered.

The experimental evidence suggests that copepodites of *Acartia* are slightly less resistant to dilution than adult females but these results should, however, be accepted with caution. The larvae did not thrive in full-strength sea water and those which attempted to moult failed to complete development, whereas the adults in general survived well. Hence the poorer salinity tolerances of the copepodites could be associated with general unhealthiness in the laboratory. The seasonal study of the development of *Acartia* conducted by Conover (1956) does, however, support the above experimental findings. Conover found that the young developmental stages began to disappear somewhat earlier than the adults, and he concluded that unfavorable changes in the environment were affecting the young stages sooner than the adult females.

Variation in salinity tolerance may also exist between the various developmental stages of a species. Thus, the mortality of Stage IV copepodites and decapod zoeae in diluted sea water differed from that of earlier copepodites and post larvae, respectively. It is interesting that differences have been recorded between the zoeal stages of both *Sesarma* and *Panopeus* crabs, and that once the megalopa is reached, a wider range of salinities is tolerated (Costlow *et al.*, 1960, 1962).

The development of *Carcinus* megalopas, *Porcellana* zoeae, and *Elminius* nauplii was delayed or prevented at the lowest salinities. Such findings endorse existing information. Thus, during attempts to rear the crabs, *Sesarma*, *Panopeus*, and *Hepatus* in diluted sea water, it is found that moulting can be delayed, development can be slower, and the duration of individual stages can be longer; at the lowest salinities, complete development to the crab stage does not take place (Costlow and Bookhout, 1959, 1962; Costlow, 1960; Costlow *et al.*, 1960, 1962). The quiescence and delayed development displayed by *Elminius* nauplii in diluted sea water can also occur amongst larvae of the barnacle *Balanus* (Barnes, 1953). Many planktonic crustaceans pass through several moults before becoming adults and it is probable that sensitivity to dilution will vary according to whether an individual is at a pre-moult, inter-moult or post-moult phase.

It is obvious that the range of salinity compatible with life can vary not only between the different developmental stages of a single species but also between one species and another. In compiling the list of salinity tolerances for zooplankton from Southampton Water, it has not been practicable to conduct exhaustive acclimation tests and therefore the ultimate survival limits controlled by the genotype (see Prosser, 1955, 1957, 1958) cannot be predicted. Even so, the experimental data do aid the interpretation of field records.

Elminius nauplii showed no mortality in dilutions above 12.3‰ whereas Barnes (1953) has deduced from experiments on barnacle nauplii that *Balanus balanoides*, *B. crenatus* and *B. balanus* are unlikely to spread into waters with salinities below 16‰. The ability of *Elminius* to withstand greater dilution could be an important factor in competition between the species, especially as a high degree of eurythermy has been attributed to *Elminius* (Crisp and Davis, 1955).

The salinity tolerances determined in the laboratory for *Acartia tonsa*, *A. bifilosa* and *A. discaudata* are in general agreement with field observations on geographical distribution (Lance, 1963). The field records for these three species were reviewed in 1963 but the additional species studied in this present paper still have to be considered:

Acartia clausi occurs around the British Isles not only offshore but also in bays and harbors of low salinity (Gurney, 1931; Wells, 1938; Conover, 1957; Raymont and Carrie, 1958, 1959). Although *A. clausi* can be plentiful at salinities as low as 18.4‰ (Farran, 1910) and withstands abrupt changes of 9–29.9‰ (Deevey, 1948), it is less tolerant of dilution than *A. tonsa* and less able to propagate in low-salinity waters (Jeffries, 1962). The distribution of *A. clausi* is world-wide, yet it appears to be the least tolerant of the four *Acartia* species.

Centropages hamatus is more common in coastal waters than in the open sea. It has been recorded at a salinity range of 23.9–13.5‰ (De Lint, 1922, cited in Gurney, 1931) and penetrates into estuarine regions around the British Isles (Gurney, 1907, 1931; Rees, 1938; Wells, 1938; Conover, 1957). This species is considered to be more neritic than *Temora* (Hansen, 1960).

Temora longicornis only penetrates estuaries where there is an active renewal of water from outside (Bigelow and Sears, 1939) and high oceanic salinities may be effective barriers to distribution (Bigelow, 1926). It occurs in British estuaries (Wells, 1938; Conover, 1957; Marine Biological Association, 1957) and has been found elsewhere at ranges of 25–31‰ (Deevey, 1948) and 6–35‰ (Bigelow, 1926).

The following order of salinity tolerance is based on experimental results: *Acartia tonsa* > *A. bifilosa* > *A. discaudata* > *A. clausi* > *Centropages hamatus* > *Temora longicornis*. This order of tolerance is also indicated by existing field observations on the extent to which different species enter and propagate in low-salinity waters. In the laboratory, *Centropages hamatus* (unlike the other species) showed poorer survival in full-strength sea water than in dilutions down to 60% sea water. Bigelow's comment (1926) that this copepod occurs chiefly in waters below 32.5‰ is therefore of special interest. The unexpected sparcity of *Centropages* in certain localities may reflect a response to different types or qualities of water (see Raymont and Miller, 1962; Provasoli, 1963).

Summary

1. The salinity tolerances of copepods varied according to the stage in the life-history. Adult males were less resistant to dilution than females (*Acartia discaudata*, *A. clausi*, *Centropages hamatus*), while copepodites appeared to be slightly less tolerant than adult females (*Acartia tonsa*, *A. bifilosa*).

2. *Carcinus maenas* zoeae showed a higher mortality in diluted sea water than the megalopa stages, whereas *Porcellana longicornis* zoeae were more tolerant than the post larvae.

3. The moulting of *Carcinus* megalopas and *Porcellana* zoeae into crabs and post larvae, respectively, and the development of *Elminius modestus* nauplii into cyprids were prevented or delayed by water of low salinity.

4. The salinity tolerances of important members of the zooplankton of Southampton Water were compared.

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